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Biological Oceanography of the Eastern Tropical Pacific: Summary of Existing Information

by Maurice Blackburn

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By

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Contribution from the Scripps Institution of Oceanography,
University of California, San Diego

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CONTENTS

	Page
Introduction	1
Material and methods	3
Chlorophyll *a*	3
Primary productivity	4
Zooplankton	4
Micronekton	5
Vertical distribution of biological properties	5
Variation in biological properties by times of day	6
Variation in biological properties on successive days	6
Horizontal distribution of biological properties	7
Seasonal (half-yearly) distribution of biological properties	11
Relationships within and between trophic levels	12
Biological oceanography of special areas	13
Taxonomic composition of standing crops	14
Ecology of special groups of organisms	14
Acknowledgments	15
Literature cited	15
Appendix	18

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ABSTRACT

Investigations of the biological oceanography of the eastern tropical Pacific are reviewed. Published papers, papers in press, and completed manuscripts, are briefly summarized. On most of the 29 biological-oceanographic expeditions made since 1952, similar properties were measured by similar methods. Numbers of available comparable measurements are: standing crop of surface chlorophyll a, 1,153; surface primary productivity, 603; standing crop of small zooplankton in the upper 300 m., 875; standing crops of chlorophyll a and micronekton in the upper 100 m., about 100 each; other types of measurements, small numbers.

The measurements of surface chlorophyll a, surface productivity, and zooplankton are analyzed by 14 areas which are distinguished on the basis of the physical structure of the upper 200 m. and by half-yearly periods irrespective of year. The analysis by areas shows that all three measurements are highest in upwelling areas (coastal and equatorial) and areas with thin mixed layers, lowest in areas with thick mixed layers (in the subtropical anticyclonic current gyrals), and intermediate elsewhere. The analysis by periods is partly inconclusive because of the uneven distribution of observations through the year. The most interesting result is the unexpected lack of statistically significant differences between property means for the 2 half-years in some of the areas which are believed (on physical-oceanographic grounds) to be seasonally eutrophic.

The paper also summarizes findings reported elsewhere on changes in biological properties with depth and time of day and on successive days. Past studies on statistical relationships between different properties measured at the same times and places and on the ecology of special groups of organisms (especially chaetognaths, considered as possible "indicators" of water masses or property-distributions) are also summarized briefly. Numerous deficiencies of knowledge are evident; increased research could contribute fundamentally to the much neglected study of biological oceanography in the tropical oceans of the world.

INTRODUCTION

This paper is a summary of biological oceanography of the eastern tropical Pacific Ocean. It is mainly a review of published papers and completed manuscripts, most of which were written by others, but it includes some material which has not appeared elsewhere. The purpose is to state the principal biological-oceanographic results obtained from the region in ways that may suggest needs for further work and the forms it should take. The emphasis is placed on modern measurements of properties of the kind that are of general interest and may be made anywhere in the ocean and on ways in which the data

Table 1.--List of operations, April 1952-March 1964, which yielded biological-oceanographic data about the eastern tropical Pacific Ocean (excludes California Cooperative Oceanic Fisheries Investigations cruises, and work done by the Inter-American Tropical Tuna Commission in the Gulf of Panama)

[C = chlorophyll a, P = primary productivity, Z = zooplankton, and M = micronekton; asterisk means data methodologically noncomparable with those of other operations]

Operation	Period	Source of data	Main kinds of data
	1952		
* 1. Galathea cruise	Apr. - May...	Steemann-Nielsen and Jensen, 1957	P*
2. Shellback	May - Aug...	Scripps Institution, unpub.	Z
* 3. H. M. Smith cruise 18	Oct. - Nov...	King and Hida, 1957	Z*
	1953		
4. N. B. Scofield cruise 53-S-1	Jan. - Mar...	Wilson and Shimada, 1955	Z
* 5. Yale South American expedition	Mar. - May...	Posner, 1957	Z*
	1954		
* 6. C. H. Gilbert cruise 15	Feb. - Apr.	King and Hida, 1957	Z*
	1954 1955		
7. Wigwam	Apr. - May...	Holmes, 1962, and unpub.	C, P
	1955		
* 8. Eastropic (H. M. Smith)	Sept. - Dec...	King, Austin, and Doty, 1957	C, P, Z, M*
9. Eastropic (Baird & Horizon)	Sept. - Dec...	Holmes, Schaefer, and Shimada, 1957	C, P, Z
10. N. B. Scofield cruise 55-S-5	Sept. - Nov...	Mais and Jow, 1960	Z
	1956		
11. N. B. Scofield cruise 56-S-1	Jan. - Mar...	Mais and Jow, 1960	Z
12. Scope	Nov. - Dec...	Holmes and others, 1958	C, P, Z
	1957		
*13. H. M. Smith cruise 38	Jan. - Mar...	Wilson and Rinkel, 1957	P, Z*
14. Island Current Survey	May - June..	Bennett and Schaefer, 1960	C, P, Z
15. Tuna Spawning Survey	July.....	Klawe, 1961	Z
	1958		
16. TO-58-1 (Scot)	Apr. - June..	Holmes and Blackburn, 1960	C, P, Z, M
17. TO-58-2	Nov. - Dec...	Blackburn, Griffiths, Holmes, and Thomas, 1962	C, P, Z
	1959		
*18. Vityaz cruise 29	Jan.....	Holmes, 1963	P, Z, M*
19. TO-59-1	Jan. - Feb...	Blackburn et al., 1962	C, P, Z, M
20. TO-59-2	Aug. - Sept..	Blackburn et al., 1962	C, P, Z, M
21. Costa Rica Dome	Nov. - Dec...	Forsbergh and Joseph, 1964	C, P, Z
	1960		
22. TO-60-1	May.....	Griffiths, MS.a[1]	C, P, Z, M
23. TO-60-2 (Step-1)	Sept. - Dec...	Scripps Institution, 1961	C, P, Z, M
	1961		
24. TO-61-1	Mar. - Apr...	Blackburn, unpub.	C, P, Z, M
25. Swansong	Oct. - Dec...	Forsbergh and Joseph, 1964	C, P, Z
	1962		
26. Esmeralda cruise	July - Aug...	Forsbergh and Joseph, 1964	C, P
27. TO-62-1 (Tempo)	Aug. - Sept..	Thomas, Holmes, Griffiths, and Blackburn, MS.[2]	C, P, Z, M
	1963		
28. Julia B. cruise	June.....	Forsbergh, unpub.	C, P
	1963 1964		
29. Shoyo Maru cruise	Oct. - Mar...	Forsbergh and Broenkow, 1965	C, P.

[1] Griffiths, Raymond C. The physical, chemical, and biological oceanography of the entrance to the Gulf of California in the spring of 1960. (Scripps Institution of Oceanography, University of California, 1964).

[2] Thomas, William H., Robert W. Holmes, Raymond C. Griffiths, and Maurice Blackburn. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: cruise Tempo (TO-62-1), August 1962. (Scripps Institution of Oceanography, University of California, 1964).

suggest, confirm, or deny hypotheses about relationships of biological properties to each other and to the physical environment. The boundaries of the eastern tropical Pacific Ocean are defined as lat. 30° N., long. 130° W., lat. 40° S., and the American coast.

Wooster and Cromwell (1958) called the eastern tropical Pacific "almost completely unknown from a scientific point of view." They pointed out that the first comprehensive oceanographic survey covering a large part of the region was not made until 1952. Biological oceanography (zooplankton only) formed part of this 1952 survey ("Shell back" expedition, see table 1). In the same year the Galathea measured primary productivity at a few stations. The biological oceanography of the region at large may therefore be said to date from 1952, although significant work of this kind was done on one much earlier expedition to a particular area [the 1931 cruise of the William Scoresby in the Peru Current (Gunther, 1936)]. The first comprehensive expedition in which biological oceanography played a large and diversified role was "Eastropic" in 1955. In 1955-61 activity in this field was considerable (table 1).

Much of the impetus for this biological oceanography was generated by biologists who were concerned with the ecology, especially trophic relationships, of commercially valuable pelagic fishes of the eastern tropical Pacific. These fishes include: yellowfin tuna, Thunnus albacares; bigeye tuna, Thunnus obesus; skipjack tuna, Euthynnus pelamis; and the Central American anchoveta, Cetengraulis mysticetus, which was formerly important as a tuna baitfish. Thus the Bureau of Commercial Fisheries and the Inter-American Tropical Tuna Commission played a major role in developing biological oceanography in the eastern tropical Pacific; from 1957 onwards, most of the Bureau's work in this field was done under contract by the Scripps Tuna Oceanography Research (STOR) Program of the Institute of Marine Resources, Scripps Institution of Oceanography, University of California. The concentration of most of this activity on the epipelagic community of organisms reflected the interest in the fishes mentioned above. Practically no work has been done on the benthic communities.

Southern Californian institutions (Scripps Institution of Oceanography, Inter-American Tropical Tuna Commission, and California Department of Fish and Game) provided the staff and equipment for most of the biological-oceanographic expeditions from 1952 onwards, including (in part) two foreign expeditions, those of the Chilean Esmeralda in 1962 and the Japanese Shoyo Maru in 1963-64. The arrangement resulted in reasonable standardization of methods in biological oceanography on these cruises. Data from certain other expeditions in or after 1952 are generally not comparable methodologically with those mentioned above and are not nearly as plentiful (for the eastern tropical Pacific) either; therefore they have not been used in this paper. These expeditions are: four cruises of the BCF (Bureau of Commercial Fisheries) Biological Laboratory at Honolulu (Hugh M. Smith and Charles H. Gilbert) including the part of "Eastropic" expedition which was based on Honolulu; the Danish Galathea cruise of 1952; a cruise by Yale University in 1953; and cruise 29 of the Soviet Vityaz in 1958-59. All operations are listed in table 1 and are henceforth referred to by their numbers in that table.

Table 1 does not include some long series of biological oceanographic cruises made off Baja California by CalCOFI (California Cooperative Oceanic Fisheries Investigations), and in the Gulf of Panama and the sea off Ecuador by the Inter-American Tropical Tuna Commission, although some of the data and conclusions are mentioned later. Nor does it include cruises made by South American organizations (e.g., Instituto del Mar del Peru) in waters close to their own coasts because I have seen no tabulated data from them.

A few errors in published values of chlorophyll a and primary productivity from operation 16 have been discovered and are corrected in the Appendix.

MATERIAL AND METHODS

The principal kinds of biological properties measured have been: standing crop of chlorophyll a, primary productivity (rate of primary production), standing crop of zooplankton, and standing crop of micronekton. Standing crop of phytoplankton has not often been reported in terms of biomass or number of cells.

The methods of making these measurements were reasonably comparable, and the work was done to a large extent by the same persons using the same equipment, in all operations except those marked with an asterisk in table 1. The methods used in the operations included here may be summarized as follows.

Chlorophyll a

The well-known method, which involves filtration, extraction with acetone, and spectrophotometric measurement of optical density of the extract, was used. Full details were given by Holmes et al. (1957), Holmes and Blackburn (1960), Forsbergh and Joseph (1964), and Holmes (MS.[1]). The concentrations, in milligrams per cubic meter of water filtered, were calculated from the equation of

[1] Holmes, Robert W. A contribution to the physical, chemical, and biological oceanography of the northeastern tropical Pacific. (Scripps Institution of Oceanography, University of California, 1964).

Richards with Thompson (1952), except those for operation 29. There the concentrations were calculated from the equation of Parsons and Strickland (1963) and are so given in the data list for the cruise (Forsbergh and Broenkow, 1965), but for the purpose of this paper they were multiplied by 1.345 (the Richards-Thompson D_{665} constant divided by the corresponding Parsons-Strickland constant) to make them reasonably comparable with the rest of the data. Data on chlorophyll a from operation 9 are ignored; only 21 measurements were made from the eastern tropical Pacific, and they may not be comparable with others because of differences in methods (King et al., 1957; Robert W. Holmes, personal communication). Night observations were omitted because of possible diurnal variation, and also because they were scanty.

Many more observations were made on chlorophyll a at the sea surface than at other depths, and on some operations (25, 26, 28, 29) only surface observations were made. (A few samples collected at depths of 1, 2, or 3 m. have been considered surface samples.) Subsurface observations were made at four to eight depths in the upper 150 m. The sampling depths were frequently the same as those used in studying vertical distribution of primary productivity; at other times they were chosen to agree with features of temperature-depth curves obtained by bathythermograph, or were arbitrary and standard (Holmes, MS., see footnote 1).

Primary Productivity

The well-known C^{14}-uptake method was used, sometimes with incubation under constant artificial illumination--the original method of Steeman-Nielsen (1952)--and sometimes under in situ or simulated in situ conditions of illumination. In situ incubation means suspension of inoculated samples from a buoy at depths corresponding to those from which they were obtained, for half a solar day immediately following collection and inoculation of samples. In simulated in situ incubation (sometimes called "deck incubation"), the samples are individually screened with neutral filters of varying density, so as to receive illumination comparable with that at the depths from which they came, and then placed in circulating sea surface water on the unshaded deck of a ship for half a solar day. Another method of in situ incubation, suitable only for surface samples, is to trail inoculated samples in the wake of the ship for half a solar day ("trailing bottle technique"). Details of these incubation techniques, and other aspects of the C^{14} method were given by Holmes et al. (1957), Holmes and Blackburn (1960), Blackburn et al. (1962), Forsbergh and Joseph (1964), and Holmes (MS., see footnote 1). The photometry to determine depths at which irradiance corresponds to that through the neutral filters was fully discussed by Holmes (MS., see footnote 1).

Only surface values (in milligrams of carbon per cubic meter per day) are used in the later sections of this paper which deal with horizontal and seasonal variations in primary productivity, since observations were much fewer at other depths. On the basis of analysis and discussion of incubation methods by Holmes (MS., see footnote 1), only in situ, simulated in situ, and "trailing bottle" observations are used. When estimates of primary productivity were available from more than one of these incubation methods at the same station, only one was used; in situ was preferred to simulated in situ, and the latter to "trailing bottle." Both Holmes and Forsbergh used dark bottles as controls to some extent in their incubations; Holmes did not routinely subtract dark-bottle values, which were usually low, but Forsbergh did (except on operation 28). Hence, the available surface data discussed are a mixture of light-bottle values and light-bottle minus dark-bottle values; they are heterogeneous also in incubation method, although they do not include any values resulting from incubations under constant artificial illumination. Measurements of primary productivity from operations 1, 8, and 13 are excluded because of constant artificial incubation. Operation 18 yielded data for 18 stations in the eastern tropical Pacific (Holmes, 1963); deck incubation was used, but because of possible differences in technique as compared with those used by Holmes and Forsbergh, this small group of observations is neglected in this paper.

Thomas (1964), who compared uptake of C^{14} with net and gross O_2 production, pH changes, and growth in phytoplankton cultures, concluded that the C^{14} method provides a reliable measure of net photosynthesis and increase in biomass both under good growing conditions and under conditions of incipient nitrogen deficiency.

Zooplankton

Most investigators in the eastern tropical Pacific--including those at the BCF Biological Laboratory, Honolulu, in the central tropical Pacific and CalCOFI investigators in the California Current region--have used the same net. This net, described by King and Demond (1953), has a mouth diameter of 1 m. and mesh-apertures of 0.65 mm. in the front and middle sections and 0.31 mm. in the rear section; volume of water strained is estimated from readings of a calibrated flowmeter in the mouth of the net.

The BCF Biological Laboratory in Honolulu has used this net in oblique hauls to a depth of about 200 m. on cruises which extended into the eastern tropical Pacific (operations 3, 6, 8, and 13 of table 1, and references there); CalCOFI agencies have used it in oblique

hauls to a depth of about 140 m. (Thrailkill, 1963); and on all other operations in the eastern tropical Pacific on which this net was used, oblique hauls were made to about 300 m. The volumes of catches from hauls made to different depths are not comparable, even when standardized to a uniform volume of water strained, for reasons given under the discussion of vertical distribution. In the later sections on horizontal and seasonal distribution, therefore, only the catches (milliliters per 1,000 $m.^3$) from oblique hauls to a depth about 300 m. have been considered; actually, because the depths reached in these hauls often differed considerably from the desired 300 m., hauls to any depth in the range 201 to 400 m. were included. These hauls were more numerous than any other kind made in the eastern tropical Pacific (except off Baja California where the CalCOFI hauling routine was used), and the greater depth range (0 to 300 m.) has the advantage that it probably minimizes diurnal variations. No distinction was made between hauls at different times of day or night. None of the results from operations 3, 6, 8, and 13 have been used.

Most of the data lists distinguish between volumes of small zooplankton and total zooplankton; the difference (frequently small or nil) is the volume of organisms longer than 5 cm. or with a volume greater than 5 ml. Only volumes of small zooplankton have been used here.

Micronekton

This category includes active animals about 1 to 10 cm. long that were generally collected with the large net and towing routine described by Blackburn and associates (1962) and Blackburn (MS.[2]).

A certain technique was used to collect micronekton. An oblique haul was made at night between about 90 m. and the surface, from a ship steaming at 5 knots, with a large net of uniform mesh-aperture about 5.5 mm. by 2.5 mm. Volume of water strained was estimated from mouth-area, distance towed, and an empirically obtained filtration coefficient. Volumes of micronekton (everything taken by the net, except sea snakes and watery planktonic animals such as tunicates and siphonophores) were expressed in milliliters per 1,000 $m.^3$ by Blackburn (MS., see footnote 2); in data lists published hitherto, only total volumes of micronekton were given. Other kinds of nets and hauls were used for micronekton on operations 8 and 18; the results could not be compared with those from the method described above.

[2] Blackburn, Maurice. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relationships to tuna. (Scripps Institution of Oceanography, University of California, 1965).

VERTICAL DISTRIBUTION OF BIOLOGICAL PROPERTIES

Holmes (MS., see footnote 1) summarized the available information about vertical distributions of chlorophyll *a* and primary productivity in the upper 150 m. of the eastern tropical Pacific. Of 108 noon-station profiles of chlorophyll *a* which were based on five or more sampling depths each, he found maxima in the upper part of the thermocline on 90, at the bottom of the isothermal layer on 5, and elsewhere within the isothermal layer on 13. Maxima appeared to be in the upper part of the thermocline on night-station profiles also, although there were only 18 stations and only 3 sampling depths to each. The data did not appear to justify generalization about the relative proportions of active and inactive chlorophyll *a* in the region of the maximum or elsewhere along the water column; neither could the author give reasons for the existence of the maximum at the depths at which it occurs. More recently, Lorenzen (1965) presented data which suggest that maxima near the top of the thermocline or in the isothermal layer are composed primarily of chlorophyll in living cells.

For 21 profiles of primary productivity incubated in situ in the eastern tropical Pacific, Holmes (MS., see footnote 1) distinguished four categories: those in which productivity decreased exponentially with depth; those with two maxima, one at the surface and one lower; those with two maxima, both below the surface; and those with rather uniform productivity in the upper 30 m. The profiles differed little below about 50 m. Holmes did not draw any definite conclusions about the reasons for the existence of such different distributions and observed that some profiles varied considerably from day to day in the same locality. He pointed out that surface inhibition of photosynthesis did not seem to be pronounced, and that production seemed to be appreciable below the mixed layer in some parts of the eastern tropical Pacific.

Holmes (MS., see footnote 1) analyzed the results of zooplankton hauls made at the same 24 stations and times of day with three opening-closing nets or samplers, hauled horizontally at particular depths. Hauls in the upper part of the thermocline or the lower part of the mixed layer were nearly always richer than hauls made near the same time deeper in the thermocline. Day and night hauls showed no obvious difference in the distribution of zooplankton.

Zooplankton hauls are generally made over standard depth ranges, irrespective of thermal structure. At three stations at which opening-closing samplers were used at six depths each, analysis of the resulting profiles of the standing crop of zooplankton showed that over the range 0 to 140 m., an average of 62 percent

by volume occurred at 0 to 70 m. and 38 percent at 70 to 140 m. (Holmes, MS., see footnote 1). Blackburn (1966) used data from Klawe (1961) to show the regression of the standing crop of zooplankton at 0 to 300 m. on that at 0 to 140 m., and vice versa, for pairs of hauls made one after the other at each of 24 stations. About 80 percent of the crop at 0 to 300 m. was located at 0 to 140 m., on average, by day or night. These data, together with those of Holmes, suggest a general distribution of zooplankton for the 0 to 300 m. water column in the eastern tropical Pacific as follows: 0 to 70 m., 50 percent; 70 to 140 m., 30 percent; and 140 to 300 m., 20 percent.

Practically no useful information has been published on the vertical distribution of the standing crop of micronekton in the eastern tropical Pacific since only the 0 to 90 m. depth range has been covered in routine hauls.

VARIATION IN BIOLOGICAL PROPERTIES BY TIMES OF DAY

The emphasis in most oceanographic cruises in the eastern tropical Pacific has been so strongly on areal coverage, that little time was available for repeated observations at different times of day at particular stations. A few observations of this kind have been made, however. Holmes and Haxo (1958) made two series of observations on surface primary productivity (C^{14} method incubated under constant artificial illumination) of samples taken every 2 or 3 hours at the same station over a 24-hour period. It was clear from both experiments that photosynthesis was less between 1800 and 0200 hours than at other times of day. The daily maximum was at 0800 to 1000 in one experiment; in the other experiment, which was imperfect, the maximum could have occurred at about the same time. The variability of surface chlorophyll *a* with time of day, investigated when the second productivity experiment was being made, showed the concentration to be "fairly constant." Shimada (1958), who measured surface productivity and surface chlorophyll *a* at a station over a 46-hour period, found that both were maximal in the early morning (about 0600 to 0900 hours) and minimal at about 1800. Maxima and minima differed for productivity by a factor of about five, and for chlorophyll *a* by a factor of about two.

The largest set of observations on diurnal change in standing crop of zooplankton is from operation 27 (Griffiths, MS.[3]), on which the ship followed a drifting surface parachute drogue about 20 days and made repetitive observations (which were considered to indicate conditions in the same surface water body or water type) close to the drogue. For small zooplankton without salps, night catches (milliliters per 1,000 $m.^3$) averaged about twice as high as day catches. For all zooplankton including salps, night catches were up to 10 times, and on average 3 or 4 times, as high as day catches. These hauls were all oblique to a depth of about 300 m.

Blackburn (MS., see footnote 2) tabulated measurements of standing crop of micronekton (milliliters per 1,000 $m.^3$) at about noon and midnight on the successive days of operation 27; midnight catches were consistently 5 to 10 times higher than noon catches; noon catches consisted almost entirely of crustaceans, whereas midnight catches included typical night-rising mesopelagic fishes and cephalopods as well.

VARIATION IN BIOLOGICAL PROPERTIES ON SUCCESSIVE DAYS

On operation 27 several biological properties were measured at the same time or times of day on about 20 successive days, as described in the preceding section. Holmes (MS., see footnote 1) made rank-difference correlation tests for time-correlated trends of standing crop of chlorophyll *a* measured at about noon each day for 2 m. below the surface, the isothermal layer (total), and 0 to 71 m. (total). Only the isothermal layer showed significant time-correlation (positive); this correlation was attributed to the deepening of the isothermal layer during the experiment. Griffiths (MS. b, see footnote 3), who made an analysis of variance of logarithms of standardized zooplankton volumes for different effects, including day and time of day, found a significant interaction between day and time of day; for a shorter period of days, in which the interaction between day and time of day was not significant, both day and time-of-day effects were significant. Blackburn (MS., see footnote 2) tabulated standardized micronekton volumes for the successive days of the same experiment, separately for noon and midnight; volumes on some days differed from those on other days by factors up to three. It should be made clear that operation 27 was deliberately carried out in a time-space situation in which it was thought that temporal changes in properties would be small.

Over the period of the same experiment, highly significant positive correlation coefficients (>0.8) were obtained between the three noon measurements of chlorophyll *a* mentioned above, both with and without transformation of the data into logarithms (Holmes, MS., see footnote 1).

[3] Griffiths, Raymond C. The variability of the volumes of zooplankton taken in oblique, paired, one-meter net hauls. (Scripps Institution of Oceanography, University of California, 1963).

HORIZONTAL DISTRIBUTION OF BIOLOGICAL PROPERTIES

Various authors have drawn attention to the broad correspondence of areas in which biological properties have high values and areas in which physical processes are known to enrich the surface layer with water from below. Among them are Forsbergh and Joseph (1964) for surface chlorophyll a and productivity, Brandhorst (1958) for zooplankton at 0 to 300 m., and Blackburn (MS., see footnote 2) for micronekton at 0 to 90 m. In this section, the geometric means of all available values of surface chlorophyll a, surface primary productivity, and standardized volume of zooplankton (0 to 300 m.) are compared for 14 different areas of the eastern tropical Pacific, separately for the periods January to June and July to December (irrespective of year). These properties are the only three which have been measured sufficiently often to justify this kind of analysis. Methodologically comparable measurements of standing crop of micronekton, and standing crop of chlorophyll a for the water column, are much fewer (slightly over one hundred of each are available for the eastern tropical Pacific), and measurements of primary productivity for the water column are fewer still (Blackburn, 1966; Holmes MS., see footnote 1, Blackburn, MS., see footnote 2).

Table 2 shows the numbers of observations of the three properties by areas, half-years, and by the operations listed (except with an asterisk) in table 1. Data from operation 27 are not included, because they form a time series, in which variation was small, in the same body of water. A few unpublished values of surface (0 to 3m.) chlorophyll a from CalCOFI cruises are included (by courtesy of R. Grigg and M. B. Schaefer).

Figures 1 to 6 show the areas, recognized on the basis of physical-oceanographic conditions:

Areas 3, 12, and 13 are regions of coastal upwelling (Gunther, 1936; Reid, Roden, and Wyllie, 1958; Wyrtki, 1963; Wooster and Reid, 1963).

Areas 5 and 10 have mean annual depth of center of permanent thermocline at < 50 m.; upwelling or similar enriching phenomena occur seasonally in some localities in area 5 (Forsbergh, 1963, and references; Blackburn, 1962); offshore equatorial upwelling possibly occurs in the west of area 10 (Wooster and Cromwell, 1958).

Areas 4, 6, and 9 have mean annual depth of center of permanent thermocline at 50 to 70 m.; equatorial upwelling occurs in area 9 (Wooster and Cromwell, 1958).

Areas 2, 7, 8, and 11 have mean annual depth of center of permanent thermocline at 70 to 130 m.; equatorial upwelling occurs in area 8 (Wooster and Cromwell, 1958).

Areas 1 and 14 have mean annual depth of center of permanent thermocline at > 130 m.

The information on depth of thermocline is from Wyrtki (1964, fig. 54). Some nonupwelling areas with similar thermal structure (e.g., areas 2, 7, and 11) are recognized separately because they represent, very broadly, parts of different surface current systems (Wyrtki, 1965). The boundaries of the areas were drawn, on the basis of this physical-oceanographic information, before the biological-oceanographic data were examined. The Gulf of California, north of lat. 25° N., has had practically no biological-oceanographic study of the kind under consideration and is therefore ignored.

The periods, January to June and July to December, were selected partly on the basis of availability of biological data and partly on the basis of physical conditions. It was desirable to divide the year into periods, each of which included reasonably large numbers of observations for several areas and which might be expected to differ in biological properties in some or all areas because of known differences in physical conditions. Availability of biological data--much scarcer than physical data and very unevenly distributed over the year--dictated a limitation to two periods and narrowed the choice of the periods.

A physical basis exists for the use of two 6-month periods. On average, the northeast trade wind is strongest and the southeast trade wind weakest about March; the opposite situation holds about August (Bjerknes, 1961, and references). Two periods can be recognized, one about November to April when the northeast trade wind is stronger than the southeast, and the other about May to October when it is weaker. These periods, which are approximate, are specified from the mean monthly positions of the Intertropical Convergence charted by Wyrtki (1965). Thus, very broadly, in November to April the amount of coastal upwelling, mean depth of mixed layer, and mean velocity of westerly surface currents can be expected to be greater in comparable situations in the northern hemisphere than in the southern; in May to October they would be expected to be greater in the southern hemisphere than in the northern. Since these physical features must affect the production and distribution of organisms, some indication of seasonal changes in biological properties might be given by a comparison of data for the two periods. The physical conditions do not vary in all areas in the way and at the periods just stated, however, and the numbers of observations are very uneven for most properties in most areas. The periods January to June and July to December gave a less uneven distribution of the data than any other 2 half-year intervals. This subdivision of the year was therefore used for want of a better one.

Table 2.--Sources and numbers of observations on surface chlorophyll a, surface primary productivity, and zooplankton (0 to 300 m.), in areas 1 to 14 (see fig.) by half-years, for all years combined.

[In each of the paired entries the figure without parentheses refers to the operation number in table 1, and the figure within parentheses is the number of observations from the operation. The figures on the extreme right of the 2 half-year columns are total numbers of observations for all operations.]

Area	January-June		July-December	
	Surface chlorophyll a			
1	7(10)	10		--
2	7(16),14(58),16(7),22(7),28(3),29(18)	109	9(15),12(10),20(3),21(4),26(2),CalCOFI(2)	36
3	7(3),16(2),19(4),24(2),28(109)	120	9(1),12(1),20(9),21(6),23(6),CalCOFI(6)	29
4	16(13),19(13),22(9),24(30),28(10),29(11)	86	9(7),12(16),17(3),20(5),21(17),23(24)	72
5	16(15),19(15),24(22),29(5)	57	9(16),12(16),17(3),20(2),21(36),23(7),29(5)	85
6	16(5),29(5)	10	9(4),12(6),21(15),23(9),25(9)	43
7	29(19)	19	9(5),26(7)	12
8	29(15)	15	9(2),26(4)	6
9	29(15)	15	9(3),23(16),25(50),26(3),29(3)	75
10	29(7)	7	9(6),23(10),25(28),29(3)	47
11	29(19)	19	9(1),23(35),25(3),26(13),29(18)	70
12		--	23(23)	23
13		--	23(20),29(7)	27
14		--	23(36),26(59),29(66)	161
	Total	467		686
	Surface primary productivity			
1	7(7)	7		--
2	7(7),14(9),16(5),22(4),28(1),29(6)	32	9(4),12(5),20(1),21(3),26(1)	14
3	16(1),19(2),28(43)	46	9(1),12(2),17(1),20(4),21(6),23(5)	19
4	16(9),19(9),22(9),24(12),28(3),29(4)	46	9(1),12(9),17(2),20(5),21(11),23(16)	44
5	16(5),19(5),24(8),29(3)	21	9(4),12(16),17(2),20(1),21(21),23(5),29(2)	51
6	16(2),29(2)	4	9(1),12(7),21(8),23(7),25(6)	29
7	29(7)	7	26(4)	4
8	29(5)	5	9(1),26(2)	3
9	29(6)	6	23(10),25(38),26(2),29(1)	51
10	29(3)	3	9(1),23(9),25(18),29(1)	29
11	29(8)	8	9(1),23(23),25(3),26(8),29(6)	41
12		--	23(18)	18
13		--	23(15),29(2)	17
14		--	23(26),26(39),29(33)	98
	Total	185		418
	Zooplankton, 0 to 300 m.			
1	2(6)	6	9(5)	5
2	2(18),14(15),16(20),22(26)	79	2(8),9(37),10(8),12(6),15(35)	94
3	16(1),19(1),22(1)	3	2(1),9(4),12(1),15(7)	13
4	2(15),16(22),19(25),22(30),24(17)	109	2(6),9(12),12(9),17(9),20(10)	46
5	4(4),11(12),16(28),19(11),24(13)	68	2(9),9(46),10(8),12(9),17(6),20(4),21(8),23(1)	91
6	2(5),4(4),11(9),16(12)	30	2(7),9(9),10(6),12(3),21(6),23(3)	34
7	2(12)	12	2(3),9(13)	16
8	2(7)	7	9(3)	3
9	2(13),4(4),11(4)	21	2(18),9(14),10(16),23(8),25(12)	68
10	4(5),11(13)	18	2(11),9(9),10(6),23(2),25(5)	33
11	2(17)	17	2(37),9(9),23(17),25(1)	64
12		--	2(12),23(7)	19
13		--	23(4)	4
14		--	23(15)	15
	Total	370		505

Figure 1, 2, and 3 show geometric means and numbers of observations, for each of the 14 areas for which data were available, for surface chlorophyll a, surface primary productivity, and zooplankton (0 to 300 m. from oblique hauls), in July to December (based on data of table 2). In these and other figures, means based on fewer than 10 observations have been omitted.

As has been explained, the data on chlorophyll a consist of all observations for the solar day and the zooplankton data consist of all observations regardless of time. Within these solar-day and full-day periods, time-connected effects can cause the properties to vary by a factor of about two (chlorophyll a) or about three or four (zooplankton); I assume that these differences approximately even out.

In figure 3, and in the corresponding figure 6 for zooplankton of January to June, the means for area 3 are not based on the data of table 2, because collections at 0 to 300 m. were so few. Instead, means for zooplankton from 0 to 140 m. were calculated for the halves of the year from data in table 4 of Thrailkill (1963) and converted into estimates for 0 to 300 m. by the use of a regression (Blackburn, 1966).

The area means for chlorophyll a (fig. 1) show the expected trends: the highest values (0.70 and 0.30 mg./m.^{3}) were for the coastal upwelling areas 12 and 13; next were areas 5 and 10 (0.19 and 0.18) in which the thermocline was closest to the sea surface; farther offshore, values declined gradually as the thermocline sank deeper below the surface, to a minimum of 0.05 in area 14; the value in area 3 was low (0.12) because little upwelling takes place there in July to December; the slightly higher value in area 9 (0.14) reflects upwelling along the equatorial divergence.

Area means for productivity (fig. 2), though based on smaller numbers of observations, are distributed in much the same way; some differences can be seen nevertheless. Area 12 was again the most productive (25.8 mg.C/m.^{3}/ day), but it was followed by area 10 (20.5), area 9 (16.5), area 5 (15.7), and area 13 (10.9). These areas were the five best for chlorophyll a,

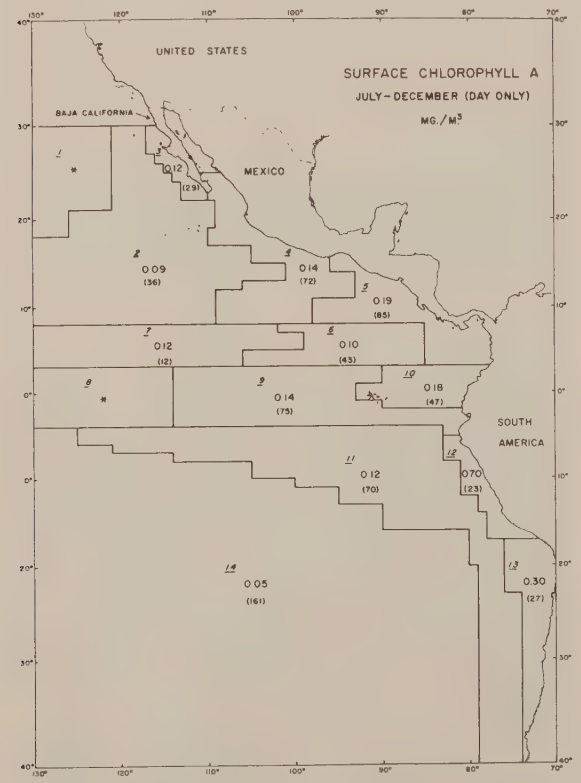

Figure 1.--Geometric means and (in parentheses) numbers of observations of surface chlorophyll a in milligrams per cubic meter, for each of the areas 1 to 14, in July to December. Daylight data only; asterisk indicates <10 observations; for further explanation see text.

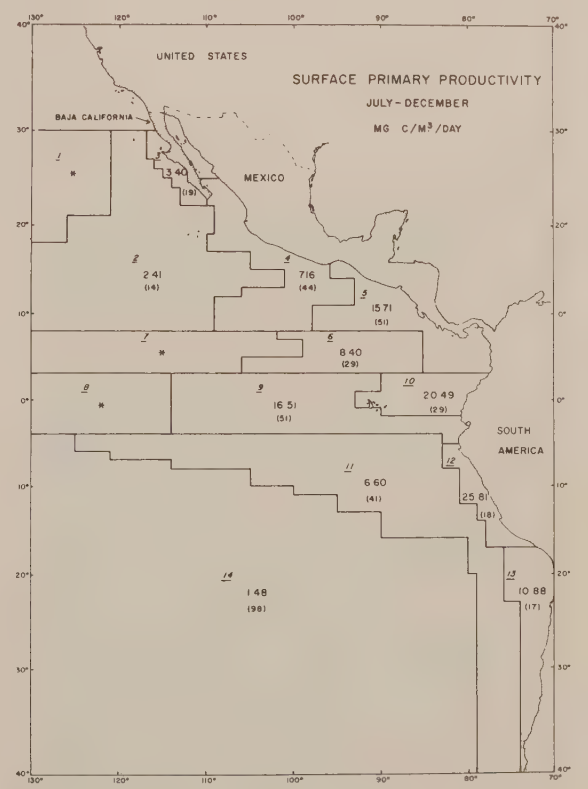

Figure 2.--Geometric means and (in parentheses) numbers of observations of surface primary productivity in milligrams of carbon per cubic meter per day, for each of the areas 1 to 14, in July to December. Daylight data only; asterisk indicates <10 observations; for further explanation see text.

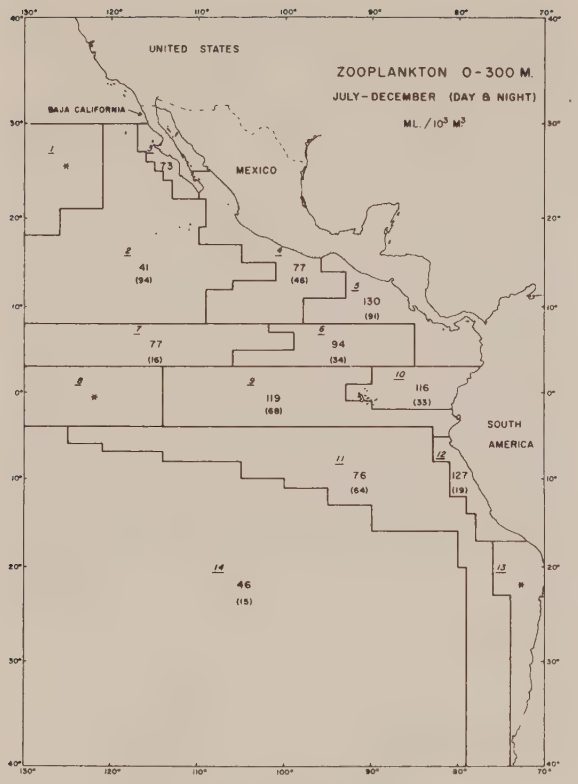

Figure 3.--Geometric means and (in parentheses) numbers of observations of zooplankton in milliliters per 1,000 $m.^3$ at 0 to 300 m., for each of the areas 1 to 14, in July to December. Day and night data; asterisk indicates <10 observations; for further explanation see text.

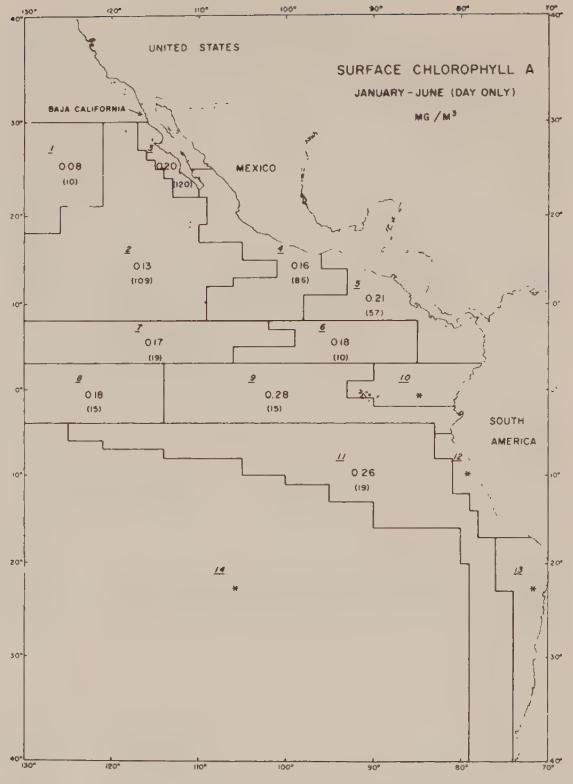

Figure 4.--Geometric means and (in parentheses) numbers of observations of surface chlorophyll a in milligrams per cubic meter, for each of the areas 1 to 14, in January to June. Daylight data only; asterisk indicates <10 observations; for further explanation see text.

but the order is different. Other values were lower; the lowest was again in area 14 (1.5).

The means for zooplankton (fig. 3) were highest in the same areas in which the other two properties were highest (no acceptable data for area 13), but the order is again slightly different ($5 = 12 > 9 = 10$). Other values were lower; area 2, not area 14, had the smallest mean.

Figures 4, 5, and 6 summarize the somewhat scantier data, corresponding to those in figures 1, 2, and 3, for January to June. Observations are lacking for areas 12, 13, and 14.

The highest means of chlorophyll a (fig. 4)--0.28, 0.26, 0.21, and 0.20 $mg./m.^3$--were in areas 9, 11, 5, and 3. Upwelling is more pronounced in area 3 at this time of year than in July to December. The reason for the high mean in area 11 is not clear. Useful data are unavailable for area 10. Means for other areas declined more or less as before, to a minimum (0.08) in area 1 which is the northern-hemisphere equivalent of area 14.

Only four area means of primary productivity were adequately based (fig. 5); the order of the areas was $3 > 5 > 4 > 2$. The mean for area 3 (27.8 $mg.C/m.^3/day$) is comparable with that for the corresponding time-space situation in the southern hemisphere (area 12 in July to December).

The order of areas according to zooplankton means (fig. 6) differed substantially from the order according to chlorophyll a. Area 10 had the highest zooplankton mean, but data on chlorophyll a were not available for that area; adequate zooplankton data were lacking for areas 8 and 1. The main similarities between area means for chlorophyll a and zooplankton were that means for areas 5 and 9 were high for both properties, and those for areas 7 and 2 low for both. Area 11 had a high chlorophyll a mean but a low one for zooplankton, perhaps because each was based on fewer than 20 observations.

Apart from these dubious means for area 11 in January to June, the distribution of means in all the figures (1-6) shows that all three biological properties tended to be highest in situations of coastal upwelling (areas 12, 3, 13), offshore equatorial upwelling (9), and shoal thermoclines (5, 10). Means were lowest in anticyclonic current gyrals where thermoclines lie deep (14, 1, 2) and intermediate in other situations (means tending to lessen with

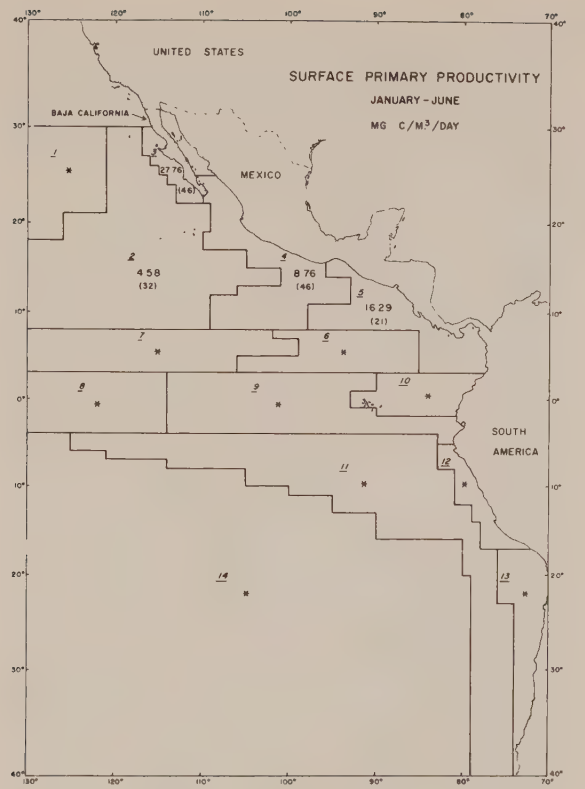

Figure 5.--Geometric means and (in parentheses) numbers of observations of surface primary productivity in milligrams of carbon per cubic meter per day, for each of the areas 1 to 14, in January to June. Daylight data only; asterisk indicates <10 observations; for further explanation see text.

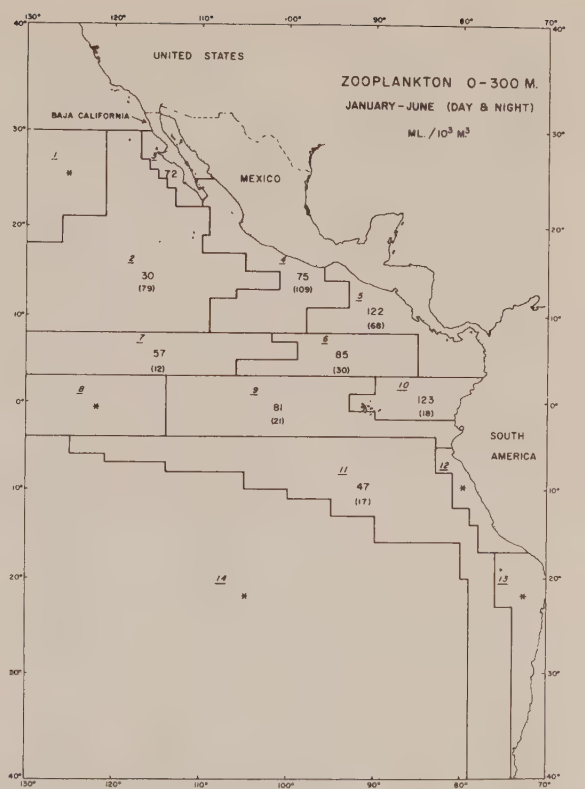

Figure 6.--Geometric means and (in parentheses) numbers of observations of zooplankton in milliliters per 1,000 m.^{3} at 0 to 300 m., for each of the areas 1 to 14, in January to June. Day and night data; asterisk indicates <10 observations; for further explanation see text.

increasing depth of thermocline). The relation to thermocline depth may be understood as follows: shoal thermoclines can be depressed by wind-mixing, so as to enrich surface waters chemically without carrying all the resulting plant crop below the compensation depth (Blackburn, 1962); in well-lighted tropical areas with shoal thermoclines, primary production can be significant below the mixed layer (Holmes, MS., see footnote 1); on the other hand, in areas where thermoclines lie deep, ascent of nutrient-rich water is unlikely, and part of whatever plant crop is formed is likely to be carried below the compensation depth. Production below the mixed layer could be expected to be more important in the eastern tropical Pacific than the eastern tropical Atlantic; both have shoal thermoclines, but the eastern tropical Pacific has fewer large rivers and is, therefore, probably less turbid.

Holmes (MS., see footnote 1) and Blackburn (1966; and MS., see footnote 2) have described areal distributions of water-column chlorophyll *a* and water-column productivity, and of micronekton. Although these distributions were based on much smaller numbers of observations than those for surface chlorophyll *a*, surface productivity, and zooplankton, they are broadly similar to the distributions of those properties as determined from more extensive data.

SEASONAL (HALF-YEARLY) DISTRIBUTION OF BIOLOGICAL PROPERTIES

Tests were made of statistical significance of difference (*t* test) between means of the logarithms of the same property for the same area for the 2 half-years, when the number of observations exceeded 10 for each period.

Tests were possible as follows: chlorophyll *a* (figs. 1 and 4), areas 2, 3, 4, 5, 6, 7, 9, and 11; primary productivity (figs. 2 and 5), areas 2, 3, 4, and 5; and zooplankton (figs. 3 and 6), areas 2, 3, 4, 5, 6, 7, 9, 10, and 11. The following differences were significant at the 5-percent level of probability: chlorophyll *a* in area 6; zooplankton in area 9. The following differences were highly significant (1-percent level of probability): chlorophyll *a* in areas 2,

9, and 11; primary productivity in area 3; and zooplankton in areas 2 and 11.

In areas 2, 9, and 11 the means for chlorophyll a were the higher in January to June, and the means for zooplankton the higher in July to December. This result is hard to understand; a lag of 6 months between maxima of standing crops of phytoplankton and zooplankton seems excessive for tropical waters (see Forsbergh, 1963), and it is not even clear why all three areas should have the chlorophyll maximum at the same season.

Area 3 had a significantly higher primary productivity in January to June (the principal upwelling season) than in July to December, as expected, but the differences between half-year means of chlorophyll a and zooplankton were not significant. Most of the data on chlorophyll a for January to June were taken late in the upwelling season; therefore, the mean may be too low. The zooplankton maximum in area 3 occurred in the middle of the calendar year, and values for other months were symmetrical around it (Thrailkill, 1963). This distribution of values seems to explain the similarity of the means for this property for the 2 half-years.

Perhaps the most interesting feature of this analysis is that no differences were significant between half-year means for areas 4, 5, 6, and 10, except for chlorophyll a in area 6. The data from areas 4 and 5 were comparatively abundant for each half-year. Surface-enriching physical processes operate seasonally in area 5, at least, and surface currents also change seasonally to some extent.

The periods January to June and July to December are not ideal for revealing differences that result from the enriching physical processes in area 5, because in the most northern part of this area, the Gulf of Tehuantepec, this enrichment occurs from about November through February (Blackburn, 1962). The biological data for area 5 were too unevenly distributed by months to permit a meaningful comparison between November to April and May to October, but they do permit a comparison between December to May and June to November; the numbers of observations for these periods are 78 and 64 for chlorophyll a, 31 and 41 for productivity, and 77 and 82 for zooplankton. None of the differences between means for these periods was significant at the 5-percent level of probability. Removal of the observations made in the eutrophic part of the Gulf of Tehuantepec (north of lat. 14°N., west of long. 94° W.) made the corresponding numbers 54 and 60 for chlorophyll a, 21 and 39 for productivity, and 59 and 72 for zooplankton; the difference between means for zooplankton was then just significant at the 5-percent level (the mean for December to May was the higher), but the other differences were still not significant.

Blackburn (1966) showed previously that regressions of standing crops of herbivores and primary carnivores upon standing crop of chlorophyll a, and partial correlation coefficients for various combinations of these three variables, were consistent with the assumption of steady-state conditions in the southern and central parts of area 5 and the eastern part of area 6. The season for these steady-state conditions could have been short (a few months preceding May, when the measurements were made) or long (possibly the whole year). It is surprising that such a situation should be found at all in a eutrophic area, for reasons given by Cushing (1959a, b). The scarcity of statistically significant differences between property means for different seasons is likewise surprising, and is again consistent with steady-state conditions even though existence of such conditions cannot be proven. Possibly the physical phenomena which produce seasonally eutrophic conditions, such as those in the Gulf of Tehuantepec, are too restricted in space and time to have much effect on standing crops and primary productivity averaged for a large area over a half-year. If it were possible to compare adequately based property means for different periods from those mentioned above, more significant differences might appear.

Further work on changes within the year obviously is needed very badly in the eastern tropical Pacific. Some of the results obtained so far do not entirely agree with expectation. Very little is known about seasonal cycles of biota in tropical oceans, as distinct from tropical neritic waters (Cushing, 1959a, b; Heinrich, 1962). Information about such cycles could be most valuable for making forecasts, identifying areas in which various hypotheses about trophic relationships could be tested (e.g., those in which steady-state conditions are assumed to exist), and probably for using in other ways. The eastern tropical Pacific would be a good section of ocean in which to make these studies because of the contrasts it seems to offer between eutrophic and oligotrophic conditions.

RELATIONSHIPS WITHIN AND BETWEEN TROPHIC LEVELS

Production of phytoplankton in the eastern tropical Pacific is more likely to be limited by nutrients than by light, but the identity of the limiting nutrient or nutrients is still in doubt. Inorganic phosphate is the only nutrient that has been measured with much regularity; charts of distribution of this property agree fairly well with those of zooplankton (Reid, 1962, and references). These charts show phosphate to be generally present in surface water of the eastern tropical Pacific at a concentration higher than that which has been found to limit diatom growth (Goldberg, Walker, and Whisenand, 1951). We may presume, therefore, that some other nutrient, perhaps nitrate,

limits phytoplankton growth in this region. Thomas (MS.[4]) established the limiting concentration of nitrate for growth of a tropical oceanic dinoflagellate and showed that surface concentrations of nitrate in the eastern tropical Pacific are generally lower than this figure. The total of nitrogen compounds available in surface sea water, including ammonia, might not be limiting, however.

Blackburn (1966) demonstrated significant positive correlations between the standing crop of chlorophyll a (water-column values) and each of the following at about the same times and places in the eastern tropical Pacific: primary productivity (in the same water-column), standing crop of certain herbivores (0 to 300 m.), and standing crop of certain primary carnivores (0 to 90 m.). The regression (slope) coefficients showed that the standing crop of herbivores varied as some power <1.0 of the standing crop of chlorophyll a. This low value of the slope suggests that efficiency of utilization of plants by herbivores decreases with increase of the standing crop of plants. On the other hand, the relation between the crop of carnivores and that of herbivores was approximately linear. The standing-crop ratios, copepods--plants (by estimated weight of carbon) and carnivores--zooplankton (by displacement volume), were both estimated roughly at 0.04, but it was clear for various reasons that the corresponding efficiency ratios of the food chain, for standing crops of all material at the appropriate trophic levels, would be higher.

Forsbergh (1963) and Holmes (MS., see footnote 1) presented values of photosynthesis-chlorophyll a ratios, which were higher in eutrophic than in oligotrophic regions. Holmes (MS., see footnote 1) gave multiple regressions of primary productivity, chlorophyll a, and standing crop of zooplankton on various combinations of physical, chemical, and biological properties, and discussed their predictive value. Smayda (1965) found significant positive regressions of primary productivity on various measures of standing crop of diatoms (number, volume, surface area, and plasma volume of cells) in the Gulf of Panama. He also found that the rate of carbon assimilation per unit of standing crop was density-dependent.

BIOLOGICAL OCEANOGRAPHY OF SPECIAL AREAS

Some detailed studies have been made of spatial and temporal changes in the distribution of biological properties in certain areas where physical processes such as upwelling or vertical wind-mixing occur.

The most thorough study of this kind was by Forsbergh (1963) for the Gulf of Panama, where observations were made about every 2 weeks for about 4 1/2 years. Coastal upwelling occurs seasonally in this area, which is neritic and not oceanic. Standing crop of phytoplankton and primary productivity were significantly greater during upwelling than during nonupwelling; about as much carbon per square meter of sea surface was fixed by phytoplankton during the 4-month upwelling season as during the remaining 8 months. Relative efficiency of photosynthesis (photosynthesis corrected to unit standing crop and unit light energy) was closely related to indices of upwelling such as temperature and salinity. Mean northerly (offshore) winds for 3 days preceding the observation day were better correlated with indices of upwelling and relative efficiency of photosynthesis than were other means. The response of photosynthesis to changes in velocity and direction of the wind seems to be rapid. The phytoplankton-zooplankton relationship was obscure.

Blackburn (1962, 1963) reported the physical and biological results of repetitive seasonal cruises to the Gulf of Tehuantepec, which is more oceanic than the Gulf of Panama. He showed that the offshore wind, which is seasonal as at the Gulf of Panama, produces a characteristic surface circulation and associated thermocline topography. The thermocline becomes so shoal in some areas that its nutrient-rich waters lie close to the surface. The mixing action of the wind itself then causes some transfer of these nutrients into the surface layer; higher standing crops of chlorophyll a and zooplankton are then produced, at or a little "downstream" from the site of the vertical mixing. Crops are much lower in other parts of the Gulf, and in all parts of it at seasons when the wind is weak.

Gunther (1936) noted that standing crops of phytoplankton and zooplankton were higher in areas of coastal upwelling than elsewhere along the coast of Peru, and Sears (1954) described the types of biological disasters that occur when the coastal waters of Peru become exceptionally warm and which have been considered to be consequences of the poorly understood phenomenon called "El Niño."

Holmes (MS., see footnote 1) drew attention to the biological richness of the Costa Rica Dome, an offshore upwelling area, and presented many measurements.

Similar investigations have been made in noneutrophic parts of the eastern tropical Pacific. Bennett and Schaefer (1960), who studied the so-called "island effect" at Clarion Island, found that primary production and the crop of chlorophyll a increased slightly towards the island, but zooplankton showed no such gradient in standing crop (the crop of zooplankton was extremely low). Griffiths' (1963) investigation of the distribution of biological

[4] Thomas, William H. Surface nitrogenous nutrients and phytoplankton in the northeastern tropical Pacific. (Scripps Institution of Oceanography, University of California, 1965).

properties in and on either side of a narrow ocean front yielded some indications that standing crops of chlorophyll a and zooplankton were highest in the front itself. Charts of distribution of standing crop of zooplankton are available for many months and years off the west coast of Baja California (Thrailkill, 1963, and references). Some broad features of these distributions have been discussed by Reid (1962) in relation to physical and chemical oceanographic properties.

TAXONOMIC COMPOSITION OF STANDING CROPS

Little emphasis has been placed on taxonomic composition of standing crops of phytoplankton, zooplankton, and micronekton in the eastern tropical Pacific. Some studies have been made of major groups within the phytoplankton (diatoms, dinoflagellates, coccolithophores: Hasle, 1960, and references). Hasle was the first worker to identify samples collected in water bottles, rather than in nets or in bottom samples, from the central or eastern Pacific. Her material was collected on operation 13, near the equator at long. 145° W., just outside the eastern tropical Pacific as defined in this paper. Coccolithophores were numerically dominant in most samples. Smayda (1963, 1965), who studied a long series of water-bottle samples from the Gulf of Panama, found that diatoms made up about 97 and 99 percent of phytoplankton biomass, and 86 and 71 percent of phytoplankton cell numbers, during the upwelling and nonupwelling seasons.

Mais and Jow (1960) tabulated the main constituents of net-caught zooplankton from operations 10 and 11, mostly taken in areas 5, 6, 9, and 10. Volumetrically, the main constituents were: copepods (20 percent), tunicates (15), chaetognaths (12), siphonophores (8), euphausiids (5), medusae (3), decapods (2), amphipods (1), and ostracods (<1). Numerically, the main constitutents were copepods (63 percent), chaetognaths (15), tunicates (6), euphausiids (5), siphonophores (1), ostracods (1), amphipods (<1), decapods (<1), and medusae (<1).

Blackburn (MS., see footnote 2) gave similar information, volumetrically only, for micronekton. For a total of 131 night hauls distributed over most of the eastern tropical Pacific except areas 1, 8, and 14, the main constituents were: galatheids (40 percent), myctophids (15), leptocephali (10), euphausiids (8), peneids (4), gonostomatids (3), enoploteuthids (3), portunids (3), larval squillids (2), sergestids (2), cranchiids (2), and postlarval and adult squillids (1). The galatheids, peneids, portunids, and squillids (postlarvae and adults) occurred mainly in particular parts of the region--the galatheids in area 3, peneids in 4, portunids in 5, and squillids in area 4--whereas the other groups were widely distributed.

ECOLOGY OF SPECIAL GROUPS OF ORGANISMS

Some attention has been given in the eastern tropical Pacific to the kind of biological oceanography which attempts to describe and explain the distribution and abundance of different taxonomic components of the biota. In this region, as in others, the general procedure of such investigations has been to compare the distributions of several species of the same taxon with each other and with various properties or features of the physical environment in such a way as to show which species are characteristic ("indicators") of specific types of water, and sometimes to explain why.

Some of the best work of this kind deals with the Chaetognatha; it was done by Bieri (1959), Sund and Renner (1959), Sund (1961, 1964), and Alvariño (1964a, b). The two papers by Sund are the most detailed. Horizontal and vertical distributions of species were compared with those of simple properties (temperature, salinity, dissolved-oxygen concentration) and with combinations of those properties, including the well-known temperature-salinity curves which are generally considered to characterize water masses. The following groups of species were distinguished: those that inhabit only one water mass, even though within it they tolerate such wide variations in properties that one might expect them to occur in other water masses also; those whose distribution appears to be determined by properties (including depth beneath the sea surface), and which are not necessarily restricted to a single water mass; and those which occur almost anywhere in the eastern tropical Pacific (Sund, 1961). The species limited to a single water mass are potentially useful, as a supplement to physico-chemical properties, in identifying water masses in regions where the boundaries change from time to time, as in the region at the southern tip of Baja California and the subequatorial region off the coast of South America. Some of the species that are related to definite properties, but not to a single water mass, are potentially useful, again as a supplement to other properties, in identifying situations where vertical motion of water, such as upwelling, has occurred. Distributions of species limited to a single water mass in the Peru region were used to confirm physical-oceanographic hypotheses about the way in which certain kinds of advection produced a Niño condition in 1958, and occurrences of species requiring only certain properties were used in the same region to confirm the identification of areas and periods of coastal upwelling (Sund, 1964).

Similar work, somewhat less detailed and less specific as to the factors that determine distribution, has been reported for the Euphausiidae of the eastern tropical Pacific (Brinton, 1962). Bathymetric distributions of euphausiids (Brinton, 1962) and chaetognaths (Alvariño, 1964a) have been well summarized for the Pacific as a whole, but more for the North Pacific than the eastern tropical Pacific.

For want of repetitive cruises at successive periods in most parts of the eastern tropical Pacific, few attempts have been made to describe and analyze changing species distributions, whether determined by distribution of water masses or by distribution of simple properties. Most of this work has been done in the northernmost part of the eastern tropical region (area 3 and adjacent waters), where repetitive cruises have been made under the auspices of CalCOFI. Differences in distribution of species between the warm period that occurred from about 1957 to 1959 and the earlier cooler period have been described and partly interpreted by Balech (1960) for phytoplankton, Alvariño (1964b) for chaetognaths, Brinton (1960, 1962) for euphausiids, and Radovich (1961) for fishes. Probably the most detailed contribution of this kind is that of Berner and Reid (1961), who explained changes in the distribution of the pelagic tunicate, Doliolum denticulatum, on the basis of its responses to sea temperature and major nonseasonal changes in temperature which occurred between 1949 and 1959, together with seasonal changes in surface currents.

Several other oceanographically detailed contributions are available for the same region. The study of Johnson (1960) on the distribution of pelagic larvae of spiny lobster is particularly interesting because it showed that recruitment of lobsters must depend upon features of circulation which retard the flushing out of larvae with the California Current. Distributions of calanoid copepod species have been charted for repetitive cruises in the California Current by Fleminger (1964). Ahlstrom (1959) dealt with vertical distribution of pelagic eggs and larvae of 46 species of fish in the same area. Studies of changing distribution of the pelagic crab, Pleuroncodes planipes, again in the California Current area, are being made at the Scripps Institution of Oceanography (Longhurst, MS.[5]).

The best-described species distributions for the eastern tropical Pacific as a whole are those of the yellowfin and skipjack tunas, which have been made known not by oceanographic work (except for larvae) but from the records of commercial fishing (e.g., Alverson, 1960); charts are available for each quarter-year since the beginning of 1951. Knowledge of ocean features which determine these distributions is still incomplete. Both temperature (which regulates range limits) and food supply (standing crops of animals at lower trophic levels, which probably determine distributions) are involved; salinity does not appear to be a factor (Blackburn, 1965). No attempt is made here to review several other works in which connections between ocean conditions and distribution or abundance of fishes were suspected or demonstrated.

[5] Longhurst, Alan R. The pelagic phase of Pleuroncodes planipes, Stimpson (Crustacea, Galatheidae) in the California Current. (Scripps Institution of Oceanography, University of California, 1965).

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APPENDIX

ERRORS IN PUBLISHED DATA FROM EXPEDITION SCOT, APRIL-JUNE 1958

The following error occurs in Holmes and Blackburn (1960):

P. 89: Entries for chlorophyll a under Station 137 refer to Station 139 on p. 90-91.

The following errors occur in Blackburn et al. (1962), on p. 162-169:

Station 13: trailing bottle value 0.604 is at 12 m., not surface.

Station 23: surface in situ value 0.658 is L, not D.

Station 49: in situ 10 m. value is 11.936.

Station 56: trailing bottle values (two sets) should be included as follows:. surface L, 6.70 and 2.04; 15 m. L, 8.82 and 1.08; 50 m. L, 1.44 and 1.59.

Station 56: in situ 30 m. value 2.734 is questionable; however, the in situ water column value 134 is correct.

Station 58: trailing bottle value 5.58 is L, not D.

Station 62: laboratory incubator 150 m. L value 2.894 should be deleted; add trailing bottle surface L value 39.28; first in situ surface L is 6.80, not 39.28.

Station 72: trailing bottle surface value 1.61 is L, not D.

Station 88: in situ 5 m. value is 0.446, not 0.0446.

Station 137: should read Station 139, 21° 05' N., 106° 16' W.; data are correct.

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